

GRASSLAND SONGBIRD NEST SITE SELECTION PATTERNS IN NORTHCENTRAL MONTANA

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ABSTRACT.—We explored nest site habitat selection patterns for six grassland passerine species in north-central Montana: Sprague's Pipit (*Anthus spragueii*), Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus saviarum*), Baird's Sparrow (*A. bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). We quantified habitat characteristics at sites chosen for nesting and compared them to randomly selected sites, both spatially and temporally. Using discriminant analysis, two species groups were discernable based on a combination of habitat characteristics, which were distinct from random sites. Nest sites had greater foliage height and density than random sites. This pattern generally was shown most strongly by Western Meadowlarks, Baird's, and Savannah sparrows. Three bird species selected nest patches (5-m radius plots centered on nests) having little or no clubmoss (*Selaginella densa*) cover, which was one of the most powerful discriminating variables in this analysis. The conservation implications of increasing clubmoss cover in relationship to nest site selection in northern Great Plains grasslands are discussed. Received 20 May 2003, accepted 15 August 2003.

Grassland bird abundance of the Great Plains has declined at a greater rate than for any other avifaunal group in North America (Knopf 1994, Sauer et al. 2001). This has been attributed to habitat conversion (e.g., cultivation and woody vegetation encroachment; Houston and Schmutz 1999), removal of native grazers and fire (Knopf and Samson 1997), and increased predation and brood parasitism (Basore et al. 1986, Davis and Sealy 2000). Avian conservation requires information on nest site habitat selection, which is virtually nonexistent for many grassland songbird species that breed in the northern prairie. Consequently, we quantified spatial and between-season nest site selection patterns for six grassland passerine species that co-occur in northcentral Montana: Sprague's Pipit (*Anthus spragueii*), Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus saviarum*), Baird's Sparrow (*A. bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Western Meadowlark (*Sturnella neglecta*). Discerning habitat differences in nest site selection may enable us to better understand how subtle changes in habitat characteristics of northern grasslands

could impact the community composition and distribution of bird species that breed there.

METHODS

Study area.—We conducted the study at Bowdoin National Wildlife Refuge in Phillips County, northcentral Montana (48° 24' N, 107° 39' W; elevation about 750 m). The study area consisted of flat to gently rolling native mixed grass prairie. The climate is continental and semiarid, exhibiting strong winds and high evaporation rates. Long term annual and seasonal (May to July) precipitation totals are 33.7 and 18.2 cm, respectively. Mean annual and seasonal precipitation totals were 30.6 and 15.5 cm, respectively, during the study. Herbaceous dominants included western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), clubmoss (*Selaginella densa*), and fringed sagewort (*Artemisia frigida*). Shrubs (*Sarcobatus vermiculatus*, *Artemisia cana*, *Ceratoides lanata*) were sparse, and trees absent, except sporadically outside the border of the study area. The study area has not been grazed consistently for >25 years. A small portion of the study area burned in 1994; otherwise, no burning events have occurred since refuge documentation began in 1936.

Nest searching.—We collected data during the summers of 1998–2001 on four study sites (26–59 ha; 180 ha total) situated 1.6–3.8 km apart around Lake Bowdoin. We searched

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these sites for nests 3–5 times per week from mid-May through mid-August in an attempt to locate all active nests. Search techniques included behavioral observations (Martin and Geupel 1993), foot flushes, and rope drags using a single, weighted 30-m length of rope with cans attached at 1-m intervals (S. Davis pers. comm.). Ropes were pulled systematically across each study site while observers carefully watched for females flushed off nests. Once located, nests were marked for relocation and monitored every 2–4 days.

Nest site measurements.—Following nesting termination, we took measurements directly at the nest (nest site), within a 5-m radius plot centered around each nest (nest patch), and at random 5-m radius plots ($n = 250$). We crossed each plot with two 10-m transects placed perpendicularly across the center of the plot, and took measurements at the nest (or center point of random plots), and at 1-, 3-, and 5-m intervals outward in each cardinal direction. Measurements included plant height, litter depth, visual obstruction, and vertical vegetation density. We estimated visual obstruction by measuring the height at which a 15-mm diameter pole was completely obscured by vegetation when viewed at a height of 1 m and a distance of 4 m (Robel et al. 1970). We quantified vertical vegetation density by summing the number of vegetation contacts on a pole held vertically at each sample point (Wiens 1969). We visually estimated the percent cover of the following physiognomic categories for each patch: bare ground, cactus (*Opuntia polyacantha*), clubmoss, forb, grass, litter, rock and gravel, sedge (*Carex* spp.), and shrub. Additional measurements at the nest included topographic slope and identification of plant species at the placement of the nest (sedges were identified to genus).

Data analysis.—We conducted statistical analyses using SPSS ver. 10.0.5 (SPSS, Inc. 1999), and we performed Box-Cox transformations using Minitab ver. 12.1 (Minitab, Inc. 1998). In addition to examining nest site differences among the six bird species, we also treated random plots as a separate, independent statistical group, allowing us to compare habitat use to what generally was available within the study area. Habitat variables first were summarized at the univariate level, mainly to report individual effect sizes. This

included a check for redundancy by estimating total correlation coefficients for all combinations of variables. Relative frequency of the dominant plant species at the nest was estimated for each bird species and differences tested for statistical significance (χ^2 test). We also performed a 1-way ANOVA on continuous variables to test for differences among bird species. We conducted *post hoc* comparisons using Dunnett's pairwise multiple comparison *t*-test, which compared each species to the means generated from random plots. Strength of association was summarized using the proportional reduction in error measure (adjusted R^2), which was interpreted as the amount of variance in each habitat variable explained by bird species. We used Goodman and Kruskal's tau (τ) as a proportional reduction in error measure for plant dominants (Agresti and Finlay 1986). We transformed data when assumptions of within-group normality and equal variances were grossly violated (arcsine for percentages <30 or >0 , Box-Cox procedures elsewhere).

We then used discriminant function analysis (DFA) to evaluate habitat differences among bird species at the multivariate level. Only statistically significant variables at the univariate level were included in the DFA. We used structure coefficients to interpret the individual functions. These are simple linear correlations between the habitat variables and discriminant functions; consequently, each function can be "named" according to the variables with the highest correlations. The use of structure coefficients as a basis for interpretation is advantageous over weighted coefficients since they are less affected by multicollinearity (Klecka 1980). The overall contribution of individual variables weighted across all significant functions was quantified using the potency index, which is a relative measure of the overall discriminating power of each habitat variable (Hair et al. 1992). Finally, we performed a classification procedure to provide a measure of strength of group separation, when considered relative to the expected classification based on chance alone. We employed jackknife procedures when testing the accuracy of the classification matrix, whereby each data case was classified using functions derived using all other data cases (SPSS, Inc. 1999).

TABLE 1. Nest sites of six songbird species and randomly selected plots in northcentral Montana, 1998–2001. All habitat variables except sedge and shrub cover differed among bird species, although the strength of association (R^2) generally was weak. Bird species was the strongest predictor of clubmoss cover, visual obstruction at the nest, and mean litter depth. For each habitat variable, the values for each bird species are compared to those of random plots (Dunnett's t test: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

Habitat variable	Sprague's Pipit		Savannah Sparrow		Grasshopper Sparrow	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Bare ground cover (%)	0.7	1.5	0.6	1.4*	0.4	0.8*
Cactus cover (%)	0.8	1.2**	1.0	1.2**	1.6	2.5
Clubmoss cover (%)	22.0	15.4	4.6	8.1***	20.1	11.9
Forb cover (%)	14.5	7.7	13.7	10.1	12.2	6.8
Grass cover (%)	50.2	12.9	65.5	16.4***	56.2	16.5
Litter cover (%)	10.9	9.8***	13.4	9.4***	6.1	3.9
Rock cover (%)	0.5	1.1	0.1	0.4***	0.8	2.6
Sedge cover (%)	1.4	3.8	0.6	2.1	1.9	4.8
Shrub cover (%)	0.5	1.6	0.5	1.8	0.8	3.0
Litter depth (cm)	11.2	8.8*	21.2	13.5***	9.4	7.6
Visual obstruction-nest (dm)	1.4	0.4***	1.7	0.5***	1.3	0.4***
Visual obstruction-plot (dm)	0.9	0.4	1.3	0.5***	0.9	0.4
Slope (°)	0.6	0.7	0.4	1.2	1.4	2.2
Plant height-nest (cm)	31.7	15.2**	34.3	12.1***	32.5	15.1***
Plant height-plot (cm)	25.9	7.2	31.6	7.4***	23.6	8.3
Vertical density-nest	4.3	3.9	5.4	3.7***	5.5	4.4**
Vertical density-plot	4.4	1.7	6.0	2.5***	4.4	1.9

We explored temporal variation in the dominant nest site habitat characteristics for Savannah Sparrows and Chestnut-collared Longspurs, relative to changes in habitat conditions encountered on the study area. We summarized degree of annual variation within bird species and interactions between bird species and random plots using the proportional reduction in error measure (adjusted R^2).

We treated the nest site (and patch) as independent sample units. Given the spatial proximity of the four study sites, statistical inference (at a significance level of $P < 0.05$) is restricted to the four study sites collectively, during the time period studied.

RESULTS

We located 544 nests during 1998–2001. Chestnut-collared Longspurs were the most abundant (48%, $n = 262$ nests), followed by Savannah Sparrows (21%, $n = 113$), Western Meadowlarks (9%, $n = 49$), Sprague's Pipits (8%, $n = 45$), Grasshopper Sparrows (8%, $n = 42$), and Baird's Sparrows (6%, $n = 33$). We took habitat measurements at an additional 250 randomly selected plots evenly distributed across years.

Univariate analyses.—The total correlation

matrix showed two sets of variables with correlations higher than $|0.7|$: clubmoss cover was negatively correlated with grass cover ($r = -0.716$), and visual obstruction at the nest was strongly correlated with visual obstruction within the nest patch ($r = 0.800$).

Metric habitat variables differed among bird species at the univariate level, except sedge and shrub cover ($P > 0.05$; Table 1). Strength of association for most variables was weak ($R^2 < 0.10$), particularly among the cover variables. However, clubmoss cover showed the greatest separation ($R^2 = 0.371$), followed by visual obstruction at the nest ($R^2 = 0.310$) and mean litter depth within the nest patch ($R^2 = 0.246$).

Over 99% of all nests were placed adjacent to or within 24 identified plant species. About 70% used needle-and-thread, western wheatgrass, or blue grama as the nesting substrate, which also were the dominant plant species (72%) on the study area. Proportional use of these plant dominants varied significantly among bird species, although the strength of association for these variables was weak (Table 2).

Multivariate analysis.—Six discriminant functions were derived, but only the first three

TABLE 1. EXTENDED

Baird's Sparrow		Chestnut-collared Longspur		Western Meadowlark		Random		R^2
\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	
0.2	0.3**	1.0	11.4	1.4	3.3	1.5	3.8	0.021
0.9	1.2	1.3	1.7*	1.4	2.1	1.8	2.4	0.022
4.8	6.5***	25.1	14.0***	5.1	7.3***	21.3	15.2	0.371
11.9	9.3	15.6	7.5*	9.7	6.4***	13.6	6.9	0.042
70.8	13.6***	48.6	1.7	70.0	14.5***	51.9	16.9	0.192
11.2	5.6***	6.0	2.7	11.0	8.4***	7.5	7.6	0.135
0.0	0.0**	0.6	2.0	0.6	1.9	0.7	2.1	0.039
0.8	2.8	1.0	2.9	0.6	2.4	0.7	1.8	0.007
0.4	0.8	0.9	5.2	0.4	1.3	0.9	2.9	0.000
21.3	12.2***	6.5	0.1	17.6	10.5***	8.9	10.5	0.246
1.8	0.5***	1.1	2.5***	1.8	0.5***	0.9	0.6	0.305
1.4	0.5***	0.7	0.3***	1.2	0.6***	0.9	0.5	0.201
0.5	0.9	0.9	0.3	1.0	2.1	0.8	1.2	0.014
34.9	8.0***	30.2	5.9***	39.1	14.5***	24.1	15.3	0.096
33.6	7.5***	24.9	7.4	31.8	10.7***	24.2	10.2	0.121
5.1	4.5	4.1	11.7	7.5	5.5***	3.5	3.1	0.058
6.3	2.5***	3.7	1.5	5.8	1.9***	4.0	2.2	0.174

were statistically significant (Wilk's lambda, $P < 0.05$; Table 3). The first two functions accounted for over 88% of the total discriminating power of DFA. The dominant habitat variables for the first discriminant function included clubmoss cover ($r = -0.697$), mean litter depth ($r = 0.629$), visual obstruction at the nest ($r = 0.746$) and nest patch ($r = 0.540$), and grass cover ($r = 0.538$). The second function was most correlated with the presence of western wheatgrass at the nest ($r = 0.382$). Overall, vegetation obstruction at the nest, clubmoss cover, and mean litter depth had the highest potency index.

The strength of the discriminant functions in separating groups is indexed by canonical correlation coefficients. The first function was the most powerful ($R = 0.654$), followed by the second function ($R = 0.555$), suggesting that the second function is nearly as important as the first function in its substantive utility. Overall, we correctly classified 54.4% of the data cases, which is greater than what would be expected by chance alone (14.3%). However, successful classifications were largely restricted to random plots and Chestnut-collared Longspurs, both of which showed a large degree of separation relative to the other bird

TABLE 2. Relative frequencies among dominant nesting substrates at nest sites of six songbird species and at randomly selected plots in northcentral Montana, 1998–2001. Among 24 plant species, blue grama, needle-and-thread, and western wheatgrass were the dominant vegetation on the study area and most frequently used as nesting substrates. Selection patterns varied among bird species, although collectively, strength of association (τ) between plant and bird species was weak. For each plant species, values for each bird species are compared to those of random plots (Bonferroni procedure: *, $P < 0.01$; **, $P < 0.001$).

Plant species	Sprague's Pipit	Savannah Sparrow	Grasshopper Sparrow	Baird's Sparrow	Chestnut-collared Longspur	Western Meadowlark	Random	τ
Blue grama	17.8	4.5	31.0*	0.0	21.1*	2.1	12.0	0.010
Needle-and-thread	40.0	17.3	35.7	15.2	39.1	16.7	30.8	0.008
Western wheatgrass	24.4	45.5*	4.8*	57.6*	8.8**	37.5	29.2	0.030
<i>n</i>	45	110	42	33	261	48	250	

TABLE 3. Discriminant function analysis of nest site habitat characteristics of six grassland bird species, northcentral Montana, 1998–2001. The first two functions accounted for over 88% of the total discriminating power of the DFA. Dominant habitat variables are presented in order of potency index.

Variable ^a /function	DF I	DF II	Potency index
Visual obstruction-nest	0.746	-0.186	0.335
Clubmoss cover	-0.697	-0.307	0.310
Litter depth	0.629	0.270	0.251
Visual obstruction-plot	0.540	0.310	0.195
Grass cover	0.538	0.211	0.184
Vertical density-plot	0.537	0.183	0.178
Plant height-plot	0.427	0.072	0.109
Litter cover	0.389	0.170	0.097
Western wheatgrass-nest	0.299	0.382	0.090
Plant height-nest	0.329	-0.265	0.081
Vertical density-nest	0.275	-0.104	0.052
Blue grama-nest	-0.182	-0.211	0.031
Needle-and-thread-nest	-0.187	-0.149	0.026
Forb cover	-0.147	-0.112	0.020
Cactus cover	-0.125	0.108	0.015
Rock cover	-0.110	-0.069	0.009
Bare ground cover	-0.098	0.087	0.008
% of variance	55.6	33.2	
Canonical correlation	0.654	0.555	
<i>P</i>	0.000	0.000	

^a Nest refers to variable measured at nest; plot refers to variables measured within 5-m radius circular plot centered on nest.

species. Conversely, none of the Sprague's Pipit and only 4.8% of Grasshopper Sparrow nests were accurately classified.

Temporal variation.—Adequate sample sizes enabled us to explore between-year variation in nest site selection for Savannah Sparrows and Chestnut-collared Longspurs (1998–2001). Among random plots, mean vegetation height ($R^2 = 0.533$) and vertical vegetation density at the patch level ($R^2 = 0.459$) showed the greatest annual variation, while litter ($R^2 = 0.107$) and forb cover ($R^2 = 0.135$) varied the least. Annual variation in nest site characteristics ranged from $R^2 = 0.455$ (litter cover) to 0.003 (clubmoss cover) for Savannah Sparrows, and $R^2 = 0.426$ (mean plant height on nest patches) to 0.035 (vertical density at the nest) for Chestnut-collared Longspurs. Strength of interactions between year and random plots for each bird species were generally weak ($R^2 = 0.006$ – 0.119) suggesting similar trends for habitat characteristics at nest and random plots (Fig. 1).

DISCUSSION

Univariate and multivariate analyses revealed similar nest site selection patterns. These patterns are best depicted at the multi-

variate level using a plot of group centroids on the first and second discriminant functions (Fig. 2). The dominant variables for the first function shared the common characteristic of increasing aboveground herbaceous production. This is indicated by positive associations with vertical structure (visual obstruction and vertical density), litter cover and depth, in conjunction with a negative association with clubmoss cover, which had very little vertical development (typically <3 cm in height). The second function was most associated with the presence of western wheatgrass at the nest. However, this function was difficult to interpret since no variable was strongly correlated to the function.

Sprague's Pipits used nest sites with relatively tall, vertically dense vegetation, and nest patches with greater litter cover and depth, while avoiding areas with prickly pear cactus cover. Our nest site data were consistent with findings reported by Sutter (1997) for southwestern Saskatchewan, although we found no evidence of selection against forb cover. Selection for vertical habitat characteristics by this species appears to be occurring at the scale of the nest site rather than the nest

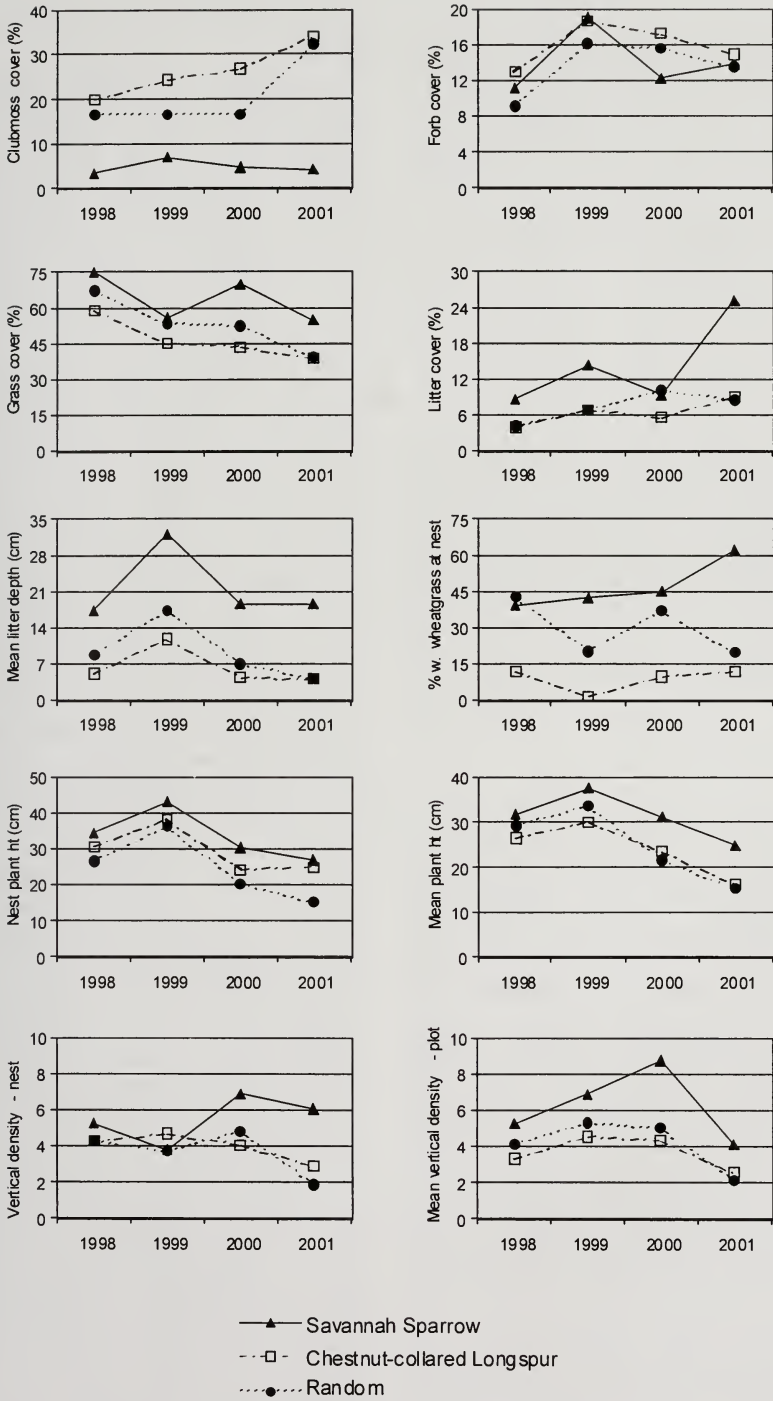


FIG. 1. Mean nest site and nest patch characteristics for Savannah Sparrows, Chestnut-collared Longspurs, and random plots in northcentral Montana.

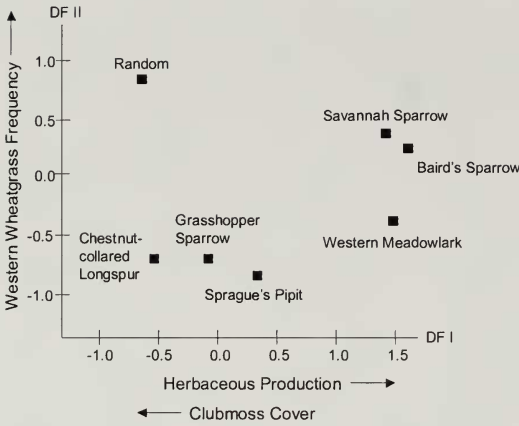


FIG. 2. Discriminant function analysis of grassland songbird nest sites, northcentral Montana, 1998–2001. Plot of group centroids for the six bird species on the first (horizontal axis) and second (vertical axis) discriminant functions. Chestnut-collared Longspurs, Grasshopper Sparrows, and Sprague's Pipits were similarly located in discriminant space, while Savannah Sparrows, Western Meadowlarks, and Baird's Sparrows formed a second, relatively cohesive group. Random plots were distinctly different from the other two groups.

patch, since these measurements were taken at both scales.

Savannah Sparrow nest patches had a well-developed litter layer, with typically little clubmoss or bare ground cover. Forb cover differed little between used and random sites, both within and among years, suggesting that this variable was merely incidental in selection. Savannah Sparrows selected several nesting habitat characteristics, but also showed great plasticity in their use, with similar trends in mean values between nest sites and random measurements. This was evident with grass cover, litter cover and depth, vertical vegetation density, and height (Fig. 2). In contrast, clubmoss cover at nest sites was consistently low across years, even though there was an apparent increase observed at random plots during 2001. This strongly suggests an avoidance of significant clubmoss cover within the nest patch. Savannah Sparrows tended to select western wheatgrass as a nesting substrate, a pattern that was relatively consistent among years, despite abrupt annual changes in the relative frequency of this grass species. This suggests that the presence of western

wheatgrass may be an important factor during selection.

In contrast, Grasshopper Sparrows generally avoided western wheatgrass as a nesting substrate, using instead blue grama. Nest patches generally were devoid of any significant bare ground cover. However, clubmoss cover at nest patches was consistent with habitat availability. Grasshopper Sparrows appear to be selecting for vertical vegetative characteristics at the immediate nest site rather than at the scale of the nest patch.

Baird's Sparrows used nesting habitat with greater litter depth and taller vegetation than expected by availability, and with nest patches devoid of bare ground, which agrees with data from southern Saskatchewan (Green et al. 2002). Baird's Sparrows also selected sites with greater grass and litter cover, with vertically denser vegetation both at the nest site and nest patch, and in particular, nest patches devoid of clubmoss. Baird's Sparrows selected western wheatgrass while avoiding altogether blue grama as a nesting substrate.

Chestnut-collared Longspurs were the most abundant species on the study area, accounting for roughly half of all passerine nests, and their nest site habitat characteristics most closely resembled general habitat conditions present on the study area. However, this species tended to avoid nest sites occupied by western wheatgrass. Chestnut-collared Longspurs also used nest sites with taller and denser vegetation than were generally available, although to a much lesser degree than the other bird species. Chestnut-collared Longspurs were the only species that generally used nest patches with greater clubmoss cover than was generally available. This was evident during 1998–2000; however, selection was not observed in 2001. Forb cover also tended to be higher at nest patches than at random plots, with the difference being consistent among years, demonstrating some plasticity in habitat use. Plasticity in habitat use also was observed for grass cover and nest substrate height. Several other variables showed little difference between used and random sites within and among years, suggesting that these variables were probably not important in selection, but instead merely incidental. These included grass and litter cover, mean litter depth, vegetation obstruction at the nest patch, and ver-

tical vegetation density at the nest site and nest patch.

Western Meadowlarks were the only species that significantly avoided nest patches with high forb cover. This species generally selected nest sites and nest patches with greater visual obstruction, vertical vegetation density and height, grass cover, and litter cover and depth, while avoiding nest patches with significant clubmoss cover.

Conservation implications.—Selection for nest sites and nest patches with greater herbaceous development than random sites and patches was shown by all species. This pattern was shown most strongly by Western Meadowlarks, Baird's and Savannah sparrows. These species generally nested in patches that had little or no clubmoss cover, which was one of the most powerful discriminating variables in this analysis. Moreover, no species used clubmoss as a nesting substrate. Consequently, clubmoss may be of particular interest concerning the condition of grasslands in the northern prairie. Although clubmoss is a natural, commonly dominant component of shortgrass and mixed grass prairie (Van Dyne and Vogel 1967), it seems evident that its cover value for nesting passerines is low. Clubmoss is an evergreen, nonflowering herb that forms dense mats that rarely exceed 2.5 cm in height (Coupland 1950, Van Dyne and Vogel 1967). It is thought to be a poor competitor with other grassland associates under relatively mesic conditions, and is not an important pioneer in disturbed areas (Crane 1990). However, clubmoss is extremely drought resistant (Webster and Steeves 1964), which allows it to successfully compete during periods of below normal precipitation (Crane 1990).

Mean clubmoss cover was 21% on our study area, which is high but within the range (6–25%) reported for mixed grass prairie in western Canada (Coupland 1950). Our estimates of clubmoss cover were fairly consistent across years, until 2001 when we observed a two-fold increase in cover. Growth rate alone cannot account for this (Dolan and Taylor 1972); rather, this increase probably is an artifact of declines in mean vegetation height and grass cover observed during 2000 and 2001, where precipitation was 15 and 29% below normal, respectively. Persistent

drought conditions may enable clubmoss to increase on the study area (Crane 1990).

While clubmoss was never used as a nesting substrate for any of the species in this study, little is known about its overall ecological role in native mixed grass prairie. Management actions to reduce clubmoss abundance include mechanical and fertilizer treatments (Smoliak 1965, Dolan and Taylor 1972), prescribed fire (Dix 1960, Wilson and Shay 1990), and grazing (Coupland 1950, Van Dyne and Vogel 1967, but see Brand and Goetz 1986). Grazing and fire are natural historical components of the northern mixed grass prairie (Knopf and Samson 1997), and have been mostly absent from Bowdoin National Wildlife Refuge for >25 years. Ironically, the absence of grazing and fire may have facilitated the development of denser and taller vegetation selected by most of the bird species studied here. Attempts to mimic natural disturbance patterns could impact current habitat characteristics selected by most members of this bird assemblage.

ACKNOWLEDGMENTS

This study was funded by the U.S. Fish and Wildlife Service, Nongame Migratory Bird Program, Region 6. Field support and resources were graciously provided by J. E. Cornely, C. R. Luna, D. M. Prellwitz, and the staff of Bowdoin National Wildlife Refuge. Special thanks go to P. J. Gouse for her technical assistance and skilled leadership in the field. Without nests, there are no analyses, so we are indebted to S. K. Davis who taught our group how to find grassland bird nests. We thank the following people for their dedicated efforts in the field: B. Adams, M. Anderson, B. S. Atchley, R. R. Conover, B. D. Gouse, J. Hammond, J. Hinz, B. G. Larson, S. N. Luttich, K. Payne, H. Sauls, C. Stahala, V. Trabold, P. N. Wiederrick, and J. K. Wood. J. Bart, R. N. Conner, and an anonymous reviewer greatly improved the quality of this manuscript. We also thank I. J. Ball, G. R. Geupel, M. T. Green, D. E. Johnson, D. H. Johnson, D. S. Klute, T. E. Martin, and R. Murphy their helpful ideas on study design.

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